



Vulnerability of biodiversity hotspots to global change

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ABSTRACT

Aim Global changes are predicted to have severe consequences for biodiversity; 34 biodiversity hotspots have become international priorities for conservation, with important efforts allocated to their preservation, but the potential effects of global changes on hotspots have so far received relatively little attention. We investigate whether hotspots are quantitatively and qualitatively threatened to the same order of magnitude by the combined effects of global changes.

Location Worldwide, in 34 biodiversity hotspots.

Methods We quantify (1) the exposure of hotspots to climate change, by estimating the novelty of future climates and the disappearance of extant climates using climate dissimilarity analyses, (2) each hotspot's vulnerability to land modification and degradation by quantifying changes in land-cover variables over the entire habitat, and (3) the future suitability of distribution ranges of '100 of the world's worst invasive alien species', by characterizing the combined effects of climate and land-use changes on the future distribution ranges of these species.

Results Our findings show that hotspots may experience an average loss of 31% of their area under analogue climate, with some hotspots more affected than others (e.g. Polynesia–Micronesia). The greatest climate change was projected in low-latitude hotspots. The hotspots were on average suitable for 17% of the considered invasive species. Hotspots that are mainly islands or groups of islands were disproportionally suitable for a high number of invasive species both currently and in the future. We also showed that hotspots will increase their area of pasture in the future. Finally, combining the three threats, we identified the Atlantic forest, Cape Floristic Region and Polynesia–Micronesia as particularly vulnerable to global changes.

Main conclusions Given our estimates of hotspot vulnerability to changes, close monitoring is now required to evaluate the biodiversity responses to future changes and to test our projections against observations.

Keywords

Biodiversity hotspots, biological invasions, climate change, conservation, land-use change, spatial prioritization.

INTRODUCTION

The current biodiversity extinction crisis is one of the major challenges that humanity faces. Future climate change is widely thought to have the potential to exacerbate both the pace and the amplitude of this crisis. In particular, novel combinations of

climatic conditions are expected across wide regions in the coming decades (Williams *et al.*, 2007; Beaumont *et al.*, 2010). Extensive evidence from the fossil record (Lorenzen *et al.*, 2011), recently observed trends (Parmesan, 2006) and predictive studies (Bellard *et al.*, 2012), all suggest that climate change is likely to have a large impact on biodiversity, from organisms to

biomes. Similarly, habitat change (loss, fragmentation and degradation) – mostly due to agriculture expansion, urbanization and grazing – is considered the greatest contemporary threat to terrestrial species worldwide. In addition, through ever-increasing public and global trade, invasive alien species (IAS) have been introduced into most ecosystems across the planet, severely affecting ecological networks, biodiversity and ecosystem functioning. The extent of the impacts of the thousands of IAS worldwide is such that biological invasions are considered the second greatest cause of biodiversity loss worldwide.

In this context, it is especially striking that relatively few studies have tried to assess the vulnerability of biodiversity hotspots to climate change, land-use changes, and IAS. Intuitively, we want to conserve the most threatened areas first, but we also want to use conservation resources as efficiently as possible (Murdoch *et al.*, 2007). One way to deal with these constraints is to identify areas that hold species found nowhere else and in which species are highly threatened; 34 hotspots have been defined as places of biodiversity vulnerability and irreplaceability (Mittermeier *et al.*, 2004). These hotspots harbour exceptional concentrations of endemic species (i.e. a minimum of 1500 endemic plant species) and have experienced exceptional habitat loss (i.e. a loss of over 70% of their original natural vegetation). Collectively, the hotspots shelter over 150,000 single-hotspot endemic plant species (over half the world's vascular plant species) and nearly 13,000 endemic terrestrial vertebrates (42% of all terrestrial vertebrates) (Mittermeier *et al.*, 2004; see also Table S1 in Supporting Information). Moreover, over two-thirds of globally threatened species are single-hotspot endemics (Mittermeier *et al.*, 2004). These regions have become international priorities for conservation, with important efforts and resources allocated for their study and preservation, possibly already in excess of \$1 billion in conservation funding (Schmitt, 2012). Despite this, the future effects of different components of global change on biodiversity hotspots have received remarkably little attention so far (but see Beaumont *et al.*, 2010, which focused on the most exceptional ecoregions, and Malcolm *et al.*, 2006, which focused solely on the effect of global warming on 25 biodiversity hotspots). Standard conservation practices may prove insufficient to maintain the biodiversity of many hotspots if only current threats are taken into account. We therefore aim to provide estimates of the future impacts of global change, which are essential for the future conservation efforts under way within these hotspots.

We examine the effects of projected future global change on 34 biodiversity hotspots for three complementary aspects. We quantify: (1) the exposure of biodiversity hotspots to climate change; (2) the vulnerability of hotspots to land modification; and (3) the future suitability of 100 IAS within the 34 biodiversity hotspots. Exposure to climate change is assessed by estimating the novelty of future climates, the disappearance of extant climates and the associated number of endemic species potentially affected; vulnerability to land-use change is assessed by quantifying changes in land-cover variables over the hotspots. Sensitivity to IAS is estimated by characterizing the combined effects of climate and land-use changes on the

future distributions of '100 of the world's worst invasive alien species'.

MATERIALS AND METHODS

Data

Climate data

Current climatic data were obtained from the WorldClim database (Hijmans *et al.*, 2005) at 10-min (0.167°) resolution and were aggregated at 30-min (0.5°) resolution for the species distribution model analyses. We selected six different climate variables linked to temperature and precipitation (see Table S2). These variables were selected because they provide a combination of means, extremes and seasonality that are known to influence the distribution of species (IPCC Core Writing Team *et al.*, 2007) and were not collinear (pairwise Pearson's $r < 0.75$). Future climate data were extracted from the Global Climate Model data portal (available at: http://www.ccafs-climate.org/spatial_downscaling/) at the same 10-min resolution. Simulations of future climate were based on three general circulation models (HADCM3, CSIRO2 and CGCM2) averaged from 2070 to 2099 ('2080'), which represent a potential increase in temperature of 3.5 °C to 5 °C. We used two different scenarios (A1B, B2A) that reflect different assumptions about demographic, socio-economic and technological development on the emission of greenhouse gases. A1B represents maximum energy requirements with emissions balanced across fossil and non-fossil sources; B2A represents lower energy requirements and thus lower emissions than A1B (IPCC Core Writing Team *et al.*, 2007).

Land-use data

Current and future global land use and land cover were simulated by the GLOBIO3 model (Bartholomé & Belward, 2005) at 0.5° resolution. The model is based on simple cause–effect relationships between environmental drivers and biodiversity impacts (for details, see Alkemade *et al.*, 2009). For the two selected emission scenarios – A1B and B2A – 30 different land-cover types from the GLOBIO3 data were aggregated into 12 land-cover types (see Table S2). We obtained the proportion of each land-cover type in 1970–2000 ('current') and 2080 for each 0.5° pixel. These data, together with climate, were used to model the potential distributions of the list of invasive species.

Invasive species data

The Invasive Species Specialist Group (ISSG) of the International Union for the Conservation of Nature (IUCN) has created a list of '100 of the world's worst invasive species', including a broad taxonomic range of species with major spread and impact worldwide, to highlight the impacts to biodiversity that these invaders can cause. In their invaded range, each of these 100 IAS threatens a large number of native species, either directly or

indirectly (Lowe *et al.*, 2000). We collected occurrence records from both the native and invaded ranges of all species using a variety of online databases, references and personal communications (Table S3). Because many records of IAS were collected between 1950 and 2000, we used current climate data for the period 1950–2000. We collected an average of 3850 records per species, with a minimum of 46 records for the least-documented species.

Climate analysis

Analysis of analogues and no-analogue climates

To determine areas that would experience climate change, we compared current climates (averaged over 1950–2000) with simulations of future climate (2070–2099). The boundaries of hotspots were originally determined by ‘biological commonalities’ (Myers *et al.*, 2000). Each of the areas features a separate biota or community of species that fits together as a biogeographical unit. We therefore made the assumption that hotspots have specific climates that explain the biodiversity found in these regions. Historical processes, contemporary ecological factors, inherent biological properties of taxa, topography, soil types and their combinations also contribute, however, to the high rates of endemism in these regions (Cowling & Samways, 1995).

We used the methodology developed by Williams *et al.* (2007) to quantify the climatic dissimilarity between current and future climate within hotspots, calculating the standardized Euclidean distance (SED) as follows:

$$SED_{ij} = \sqrt{\sum_{k=1}^6 \frac{(a_{kj} - b_{ki})^2}{S_{kj}^2}} \quad (1)$$

where a_{kj} and b_{ki} are the 1950–2000 (‘current’) and 2070–2099 (‘future’) means for climate variable k at grid points i and j (10-min resolution), and s_{kj} is the standard deviation of the intra-annual variability for 1950–2000. The standardization values were metrics of seasonality for temperature and precipitation variables. Standardizing each variable places all climate variables on a common scale (Veloz *et al.*, 2012).

We then calculated a SED threshold (SED_t) for each hotspot to discriminate the limit above which the climate was no longer considered analogue to the current conditions (i.e. climate loss). SED_t was determined by comparing the distribution of SED values between the hotspot and the rest of the world for 20th-century climate. We used the receiver operating characteristic (ROC) to determine the SED_t value that provides the optimal separation within and between surface histograms (Oswald *et al.*, 2003) (see Fig. S1). Each SED_t is therefore associated with an evaluation of the threshold (i.e. area under the curve). Four biodiversity hotspots were excluded from analysis because the low value of their AUC (i.e. less than 0.6) indicated that the critical threshold cannot discriminate between analogue and no-analogue climates (Guinean forests of West Africa, Mountains of Southwest China, New Caledonia and Cerrado). For

four very large hotspots (Horn of Africa, Indo-Burma, Mediterranean Basin and Sundaland), the threshold was averaged on the basis of 10 random samples of 10,000 values of each SED. All threshold values are presented in Table S4.

Using these SED_t values, we calculated two indices of climatic risk for each hotspot, based on an identical metric of multivariate dissimilarity. We calculated (1) the climatic distance between the end-21st-century simulation for each hotspot grid point and its closest analogue from the global pool of 20th-century climates (i.e. an index of the novelty of future climates within the hotspot), and (2) the climatic distance between the 20th-century realization for each hotspot grid point and its closest 21st-century climatic analogue (i.e. an index of disappearance of extant climates within the hotspot). For more details about the method, see Williams *et al.* (2007) and Veloz *et al.* (2012).

Assessing climate-change impacts on endemic species

We performed the climate analysis within the hotspot, assuming that its limits define the limits of climate suitability for its endemic species. Under this assumption, we considered that a loss of analogue climate within the hotspot corresponds to a loss of habitat for endemic species. Species may nonetheless be forced, and able, to move outside these limits to find suitable climate conditions in the future. In those cases (assuming such migration is unhindered), the number of endemic species threatened by climate change would have been overestimated (except for insular hotspots, where such migration is prevented by the geographical barriers of the oceans). We therefore extended this analysis of climatic risk to a radius of 500 km around each hotspot (except for insular hotspots), to conservatively identify novel and disappearing climates (Williams *et al.*, 2007). The value of 500 km was chosen conservatively, as it greatly exceeds the highest known rates of plant migration during the last deglaciation (Williams *et al.*, 2007). As a proxy for the distance a species might need to travel to maintain an equilibrium with its currently occupied climate space, we calculated the geographical distance between the current analogue climate and its closest analogue for the present, and compared it to the geographical distance between the current analogue climate and its closest analogue in the future. This value gives an indication of geographical distance between closest analogues currently and in the future.

We evaluated the number of endemic species potentially threatened by climate change by measuring the extent of the loss of analogue climate within the hotspot using the endemics–area relationship (EAR). Ecologists and biogeographers have long recognized that species richness (S) increases with area (A) at a decreasing rate and thus eventually levels off (Rosenzweig, 1995). The curve that correctly describes the rate of extinction as habitat area decreases is the EAR (Harte & Kinzig, 1997). Here, we assumed that the loss of area of analogue climate within a hotspot is a proxy of potential habitat loss for species in that hotspot. We thus used the EAR to quantify the potential number of endemic species that will be affected by a loss of analogue climate. The EAR was chosen instead of species–area

relationships (SAR), because predictions from SAR sometimes overestimate the number of extinctions (Kinzig & Harte, 2000). To derive a more realistic relationship under this possibility, EAR takes into account the number of species expected to be confined to smaller patches within the total area of habitat loss. We calculated the number of endemic species (i.e. $f_{\text{lost-EAR}}$) that is expected to be vulnerable to climate change as follows:

$$f_{\text{lost-EAR}} = (\Phi_A)^{z'}, \quad (2)$$

where Φ_A is the ratio of current analogue climate lost ($A_{\text{future}}/A_{\text{current}}$), with A_{current} the current area of the hotspot, A_{future} the remaining area with current analogue climate (i.e. where SED values are below the critical threshold that discriminates analogue to current climate versus non-analogue) and z' is a constant [$z' = -\ln(1 - 1/2^z)/\ln(2)$]. We used three different values of z : the typical value of fragmented habitats ($z = 0.25$; Brooks *et al.*, 2002); a conservative value more typical of continental situations ($z = 0.15$; Malcolm *et al.*, 2006); and an intermediate value ($z = 0.2$; Bergl *et al.*, 2007).

Land-use analysis

For both scenarios, we intersected our gridded projections of land use at 30-min resolution (0.5°) with the boundaries of the 34 hotspots. We then calculated the average proportion of each land-use class in each pixel per hotspot for the current and future periods. We calculated the percentage of changes per hotspot according to the different land-cover classes between '2000' and '2080' for the two emission scenarios.

Invasive species distribution modelling

We modelled the potential distribution of the invasive species in the 34 hotspots by combining the available occurrences with a set of climatic and land-use variables that we assume explain these species distributions (Bellard *et al.*, 2013; see Appendix S1 for details). We used six different SDMs implemented within the BIOMOD 2.0 platform (Thuiller *et al.*, 2009). We evaluated the predictive performance of each model using a fourfold repeating-split sampling approach in which models were calibrated on 70% of the data and evaluated over the remaining 30% records. The models were evaluated with both the true skill statistic (Allouche *et al.*, 2006) and the area under the ROC curve (Fielding & Bell, 1997). The final calibration of models used all the available data and was obtained by calculating the weighted mean of the distribution for each algorithm. To make sure no spurious models were used in the ensemble projections, we only kept the projections for which the model's evaluation estimated by AUC and TSS were higher than 0.8 and 0.6, respectively (e.g. Bellard *et al.*, 2013), and a weight proportional to the TSS evaluation was associated to each model. We then transformed the probability maps obtained from the ensemble projections into binary suitable/non-suitable maps at 30-min resolution (0.5°) using the threshold maximizing the TSS for each species.

All data processing and statistical analyses were performed using R 2.15 (R Core Team, 2012). We used the shapefiles of biodiversity hotspots produced by Conservation International (2011).

RESULTS

Climate change within biodiversity hotspots

Our analysis suggests that 68% to 93% of the existing climate within hotspots should remain stable in the future. The average fraction of land area per hotspot with novel climate was about 16%. The distributions of these novel climates were strongly concentrated in three hotspots: Polynesia–Micronesia (98%), Mesoamerica (65%) and the East Melanesian Islands (43.4%). The same three hotspots concentrated the largest proportions of disappearing climate, with 99%, 68% and 41%, respectively. On average, hotspots may experience 31% loss of analogue climate in the future. The distribution of novel and disappearing climate were principally concentrated at low latitudes, and decreased polewards (Fig. 1a). Using areas with a loss of analogue climate as a proxy for habitat loss, we calculated that climate change might negatively influence 25% of endemic species (with $z = 0.2$; Fig. 1b) per hotspot on average. The numbers of endemic species potentially affected by climate change were only slightly affected by the z -value (Kolmogorov–Smirnov test: $P > 0.05$ for all paired tests; Tables S5 & S6). The absolute numbers of endemic species vulnerable to climate change were 5362 in Sundaland, 3540 in the Mediterranean Basin, 3309 in Polynesia–Micronesia and 3215 in Madagascar. The closest analogue climate for any point in any continental hotspot was predicted to become three times further away than it is currently (Fig. S2). The Mediterranean Basin may be the most affected hotspot in this regard, with distances to the closest analogues increasing by up to 1145 km in the future.

Land-use changes in the hotspots

Globally, among the 12 different land-use classes, three classes showed major changes between current and future periods (Fig. 2). Over the next decades, herbaceous cover might change by -1.3% of their current cover. In contrast, non-natural areas such as mosaic habitat and pasture areas might increase in the next decades by 2.5% and 7.9%, respectively. The Horn of Africa, Madagascar and the Indian Ocean islands, the Mountains of Southwest China and the Succulent Karoo might lose at least 20% of their herbaceous cover. In addition, some hotspots – such as the Mountains of Southwest China – were predicted to have an important increase ($> 25\%$) in their pasture cover.

Biological invasions in the hotspots

All hotspots were predicted to be currently suitable for an average of 16.8 ± 8.5 IAS (i.e. invasion of at least one pixel of the hotspot) (Fig. 3a). These results are robust regarding AUC and

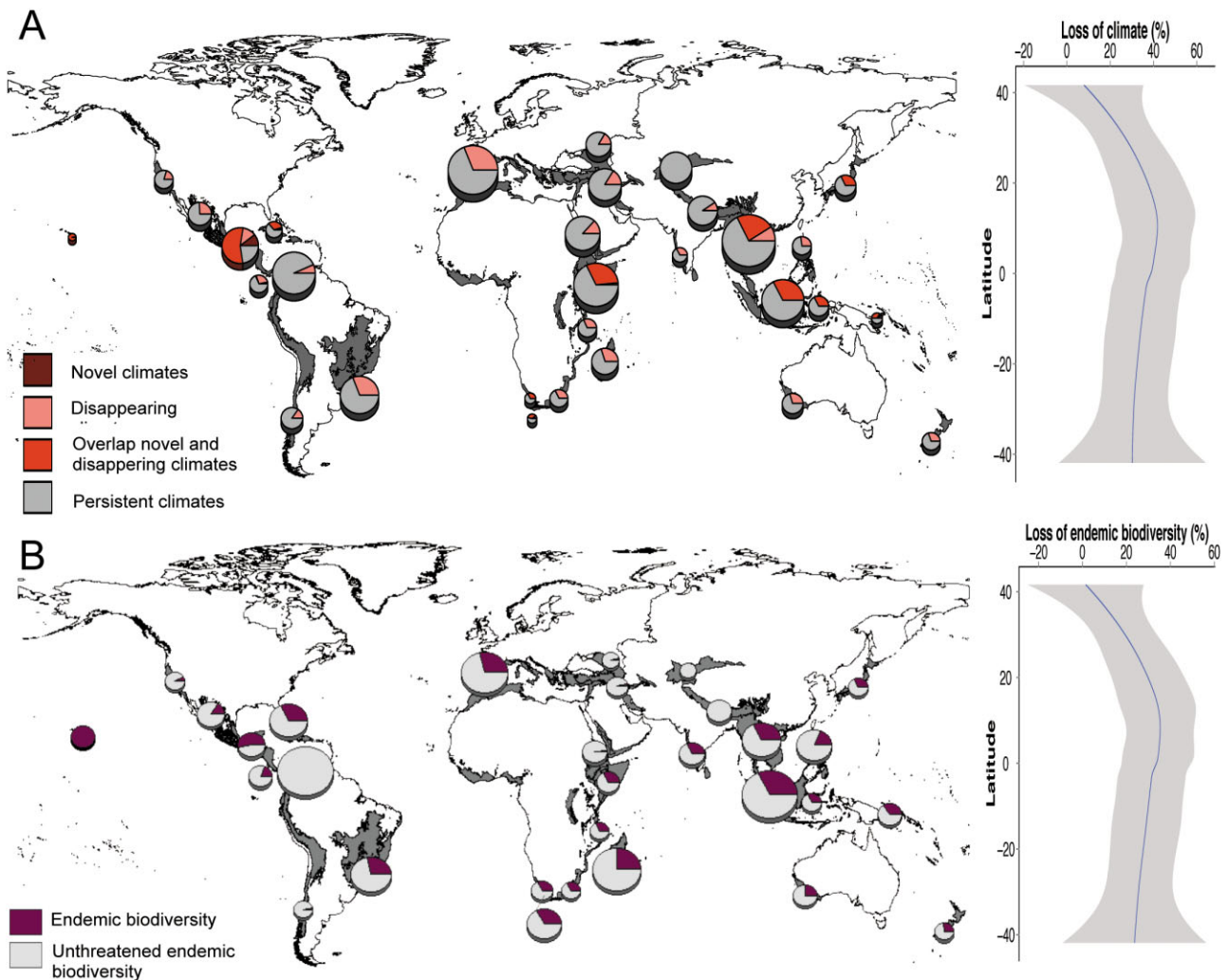


Figure 1 (a) Analogue climate loss and (b) showing the proportion of endemic species threatened by loss of analogue climate, in 2080 under the A1B emissions scenario. The size of the pie represents the area of each hotspot (note the smaller pie for Polynesia–Micronesia) (a) and the number of endemic species included per hotspot (b). The right-hand graphs show the slight effect of latitude on climate change and on biodiversity loss; the smooth curve had been performed with a LOESS (locally weighted scatterplot smoothing) method and the confidence interval represents the standard error.

TSS values (Fig. S3). In the future, most of the hotspots will be suitable for fewer IAS than currently, although the absolute number will remain very high (Fig. 3b). Surprisingly, Mesoamerica, the Caribbean islands, the Coastal Forests of Eastern Africa and the Mediterranean Basin will probably be threatened by 5–10 fewer IAS than currently. Both among and within hotspots, we found interesting spatial variations in the areas potentially suitable to IAS, especially regarding the number of species with suitable conditions (Fig. 4a,b). Globally, the average number of IAS per pixel could vary from two (e.g. mountains of Central Asia) to 34 (e.g. Caribbean islands). Five hotspots were predicted to be particularly suitable to high numbers of IAS in the future: New Caledonia, Polynesia–Micronesia, New Zealand, and the Philippines. Interestingly, those five hotspots are mainly islands or groups of islands. Furthermore, much of Central America and the South Atlantic forest were likely to be decreasingly at risk, as was the case for the northern part of the

Mediterranean Basin, Southeast Asia and New Zealand's North Island.

DISCUSSION

Our study adopted an original global approach, with the analysis of (non)-analogue climates, changes in land-use and vulnerability to '100 of the world's worst invasive alien species' in the richest and most threatened biodiversity regions around the world. Our findings showed that climate change, land-use change and biological invasions are all likely to have significant effects on biodiversity hotspots. In addition to the fact that climate dissimilarities are more important in hotspots than in the rest of the world (Williams *et al.*, 2007), hotspots suffer from significant land-use changes and are suitable for at least twice as many IAS per pixel than the rest of the world, both currently and in the future (Fig. S4).

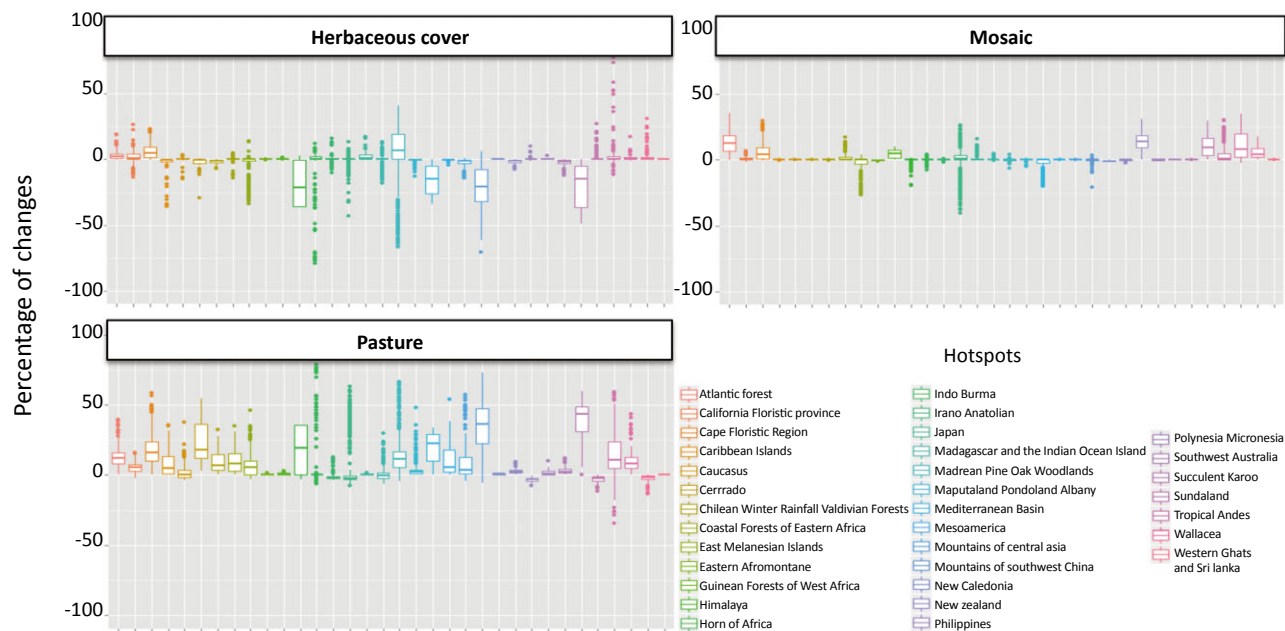


Figure 2 Percentage change in area for herbaceous cover, pasture and mosaic habitats between the current and future (2080) period under the A1B emissions scenario.

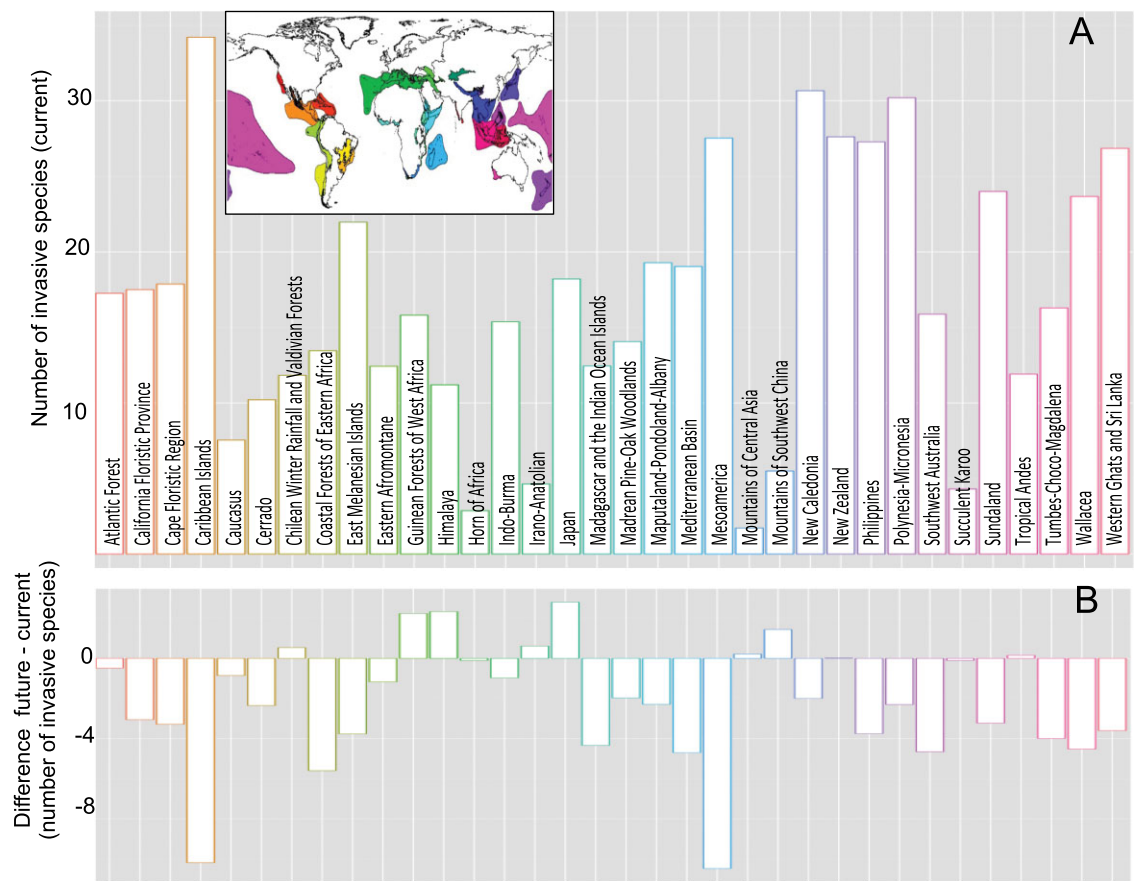


Figure 3 (a) Average number of invasive species that have suitable climatic and land-use conditions for the current period per hotspot. (b) Difference between the current and future (2080) periods in term of number of invasive species per hotspot under the A1B emissions scenario.

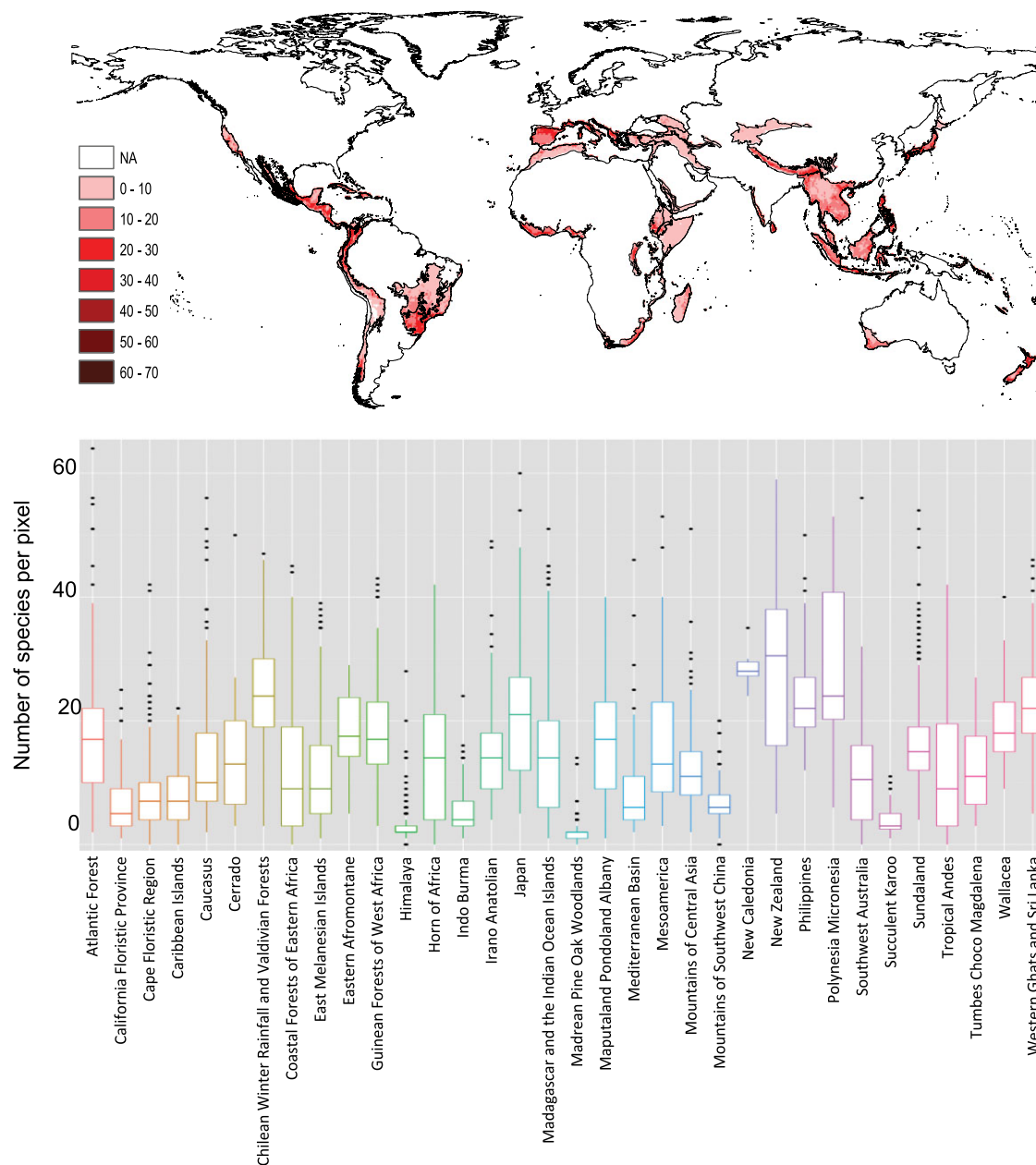


Figure 4 (a) Map representing the number of invasive species that will find suitable environmental conditions per pixel (0.5° resolution) in the 34 hotspots by 2080. (b) Boxplot of the number of invasive species per pixel for the 34 different hotspots. The upper and lower hinges correspond to the 25th and 75th percentiles, respectively, the bar represents the median value, and the points are outliers.

One possible explanation for the high vulnerability of hotspots to IAS is that hotspots are already highly disturbed, with only 30% of primary vegetation remaining. IAS thriving in disturbed habitat may therefore be particularly favoured in biodiversity hotspots compared to other, less disturbed parts of the world. It is, however, important to stress that the mere number of these major IAS predicted to find suitable environmental conditions is not a sufficient indicator of the consequences of invasions (McGeoch *et al.*, 2010). For example, there are cases of a single invasive species or a few highly invasive species altering ecosystem function. In the South African

fynbos, a few invasive woody species have led to the emergence of a novel functional type that threatens biodiversity in mountain catchments (Brooks *et al.*, 2004). Similarly, the invasion of a few species of fire-prone grasses (e.g. *Cortaderia selloana* or *Bromus tectorum*) can increase fire regimes, with dramatic consequences for the local communities (Grigulis *et al.*, 2005). Thus, although it is possible that a few invasive species can have a disproportionate impact on native ecosystems, a high number of IAS will almost certainly lead to a severe impact, thereby making our predictions relevant for the conservation of these regions.

Hotspots may also experience significant losses in analogue climates in the future (31%), and these losses may be particularly important at low latitudes. The predicted decrease in invasive species number at low latitudes may thus be partly explained by the high proportion of novel climate predicted in these areas. Furthermore, in order to find the closest suitable climatic conditions, species unable to adapt to the new conditions will have to migrate more than 1000 km. Because some hotspots are coastal, some species will be limited by water, leading to dramatic consequences if species are not able to adapt rapidly. Our results were consistent for IAS and land-use analyses regarding the two CO₂ emission scenarios, although we observed some differences for analogue climate analyses (see Supporting Information).

Although we tried to minimize the inherent uncertainties associated with our analysis, not all possible uncertainties were taken into consideration. First, our study made the assumption that the extent of analogue modern climate exerted strong influences on endemism and may lead to an increase of the hotspot vulnerability regarding endemic species when such climates change. The lack of current analogues for future climates limits our ability, however, to validate ecological model predictions (Williams *et al.*, 2007), and the used endemics–area relationship remains a coarse estimation of species that are susceptible to be affected in the future, particularly, because *z*-values are known to vary across taxonomic groups (Horner-Devine *et al.*, 2004). Moreover, climate change has occurred historically with glacial and interglacial cycles and all endemic species have had to contend with this in the past. Some endemic species may therefore have broader climatic tolerances than are represented by the available climate space within contemporary hotspots and may be able to adapt to future conditions (Lavergne *et al.*, 2010).

In addition, our analysis of IAS was based on correlative species distribution models, which have been criticized because of their inherent uncertainties, especially when applied to invasive species (Gallien *et al.*, 2010; Jiménez-Valverde, 2011; Bellard *et al.*, 2013 for further information). Important progress has been made in integrating key fitness components such as survival, growth, development and reproduction that vary with climate conditions (Estes *et al.*, 2013). The appropriate data with which to calibrate these models can, however, be expensive and time-consuming to obtain and is rarely readily available, particularly for global analyses. Until more mechanistic approaches are further developed, and the necessary data are obtained, species distribution models remain an appropriate approach to evaluate the consequences of future changes on large scales (e.g. taxonomic or geographical) and can serve as hypotheses that other approaches can test at relevant scales. The availability of presence data is a key constraint when using species distribution models. To maximize the quality of predictions, we encompassed the entire range of each species, comparing the distribution from many global databases and we included both the native and invaded ranges of species (Gallien *et al.*, 2010). Although some spatial bias appeared in the data collected (i.e. almost no IAS occurrences in northern Russia, northern Canada and the western Sahara Desert), the entire world was covered

(Fig. S5) and all the hotspots were well covered by sampling effort. In addition, we applied a modelling protocol that was robust (e.g. Araújo & New, 2007; Thuiller *et al.*, 2009) to limit the inevitable uncertainties associated with presence-only data and niche-modelling techniques (Wiens *et al.*, 2009). The most important limitation with respect to modelling IAS is that the models assume that species are in equilibrium with their environment, which is not necessarily the case here. Furthermore, the full range of suitable climatic conditions may have been underestimated, because invasive species could occupy distinct climatic conditions in invaded areas (Broennimann *et al.*, 2007; but see Petitpierre *et al.*, 2012 for plants). Additionally, the average time for invasive neophytes in Europe to reach their maximum range is about 150 years (Gassó *et al.*, 2010); the full climatic niches of many recent invasions may not therefore have been captured by the current distributions. We also did not consider the propagule pressure, biotic interactions or soil properties – all factors that may be associated with the subsequent establishment of invasive species (Hof *et al.*, 2012; Bacon *et al.*, 2013). We therefore probably overestimated the number of invasions that are likely to occur (regarding these 99 IAS), especially because many of these species may never be introduced in suitable areas. In addition, we only focused on the suitability of hotspots to these IAS, but did not consider the potential ecological, economic or health impacts of these species and how these impacts may evolve following climate change. Despite this, there is no *a priori* reason to believe that the impacts of these 99 species (which are among the worst in the world in terms of impact) would be of any less ecological magnitude for the hotspots than for ecosystems where they have been assessed. Overall, the methods used here provide some useful insights into relative vulnerabilities of the hotspots to these threats, but we are not yet able to fully understand how these systems will change under these drivers, and thus a monitoring approach is imperative.

Despite these uncertainties, our assessments have profound consequences for conservation in biodiversity hotspots. Our analyses highlight the urgent need to explicitly incorporate global change into future conservation within the hotspots (Pressey *et al.*, 2007). More precisely, a paradigm shift to first target the regions of greatest threat under global change and then to take into account both biodiversity harboured by these regions and level of protection seems particularly necessary. The three drivers of global change we studied here imply very different strategies for conservation. Climate change is now inevitable and its effects on biodiversity ought to be minimized, in part by facilitating native species' movements to more climatically suitable areas (Hodgson *et al.*, 2009). Establishing protected areas that remain resilient to climate and land-use change is a further challenge. Species movement may be impossible in heavily fragmented habitats (especially on islands) and the rate and magnitude of climatic change is such that many endemic species may be unable to disperse quickly enough. For these species, one adaptation strategy might be to translocate to other locations where the climate is suitable (Thomas, 2011). In addition, land-use changes may both complicate species movement through

increasing fragmentation and facilitate the establishment of IAS through increasing habitat disturbance. In contrast, biological invasions are still avoidable and the most efficient conservation actions have been shown to be the prevention of introduction and a rapid response (Simberloff *et al.*, 2013). Ultimately, other key drivers of biodiversity loss, including fire regime or rising atmospheric CO₂, are likely to affect biodiversity hotspots; the threat to each hotspot is therefore likely to be unique.

To conclude, the threats posed by global change are clearly a concern for all 34 biodiversity hotspots. This theoretical estimation of hotspot vulnerability based on their exposure to climate change, land-use changes, and biological invasions now requires close monitoring, in order to evaluate the biodiversity responses to future changes and to test our projections against observations. Moreover, the integration of mechanistic approaches and an increased focus on understudied drivers of biodiversity change should also be a priority.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Methodological choice of the threshold.

Figure S2 Geographical distance (km) to the closest analogue climatic conditions between the current and future periods for

the 21 continental hotspots for (a) the A1B emission scenario and (b) the B2A scenario.

Figure S3 Boxplots of TSS and ROC values for the ensemble forecast projected model.

Figure S4 Number of invasive alien species per pixel in the 34 hotspots compared to the rest of the world, for both current and future periods (A) A1 scenario on the left (B) B2 scenario on the right.

Figure S5 Combined occurrences of 99 of 'the world's worst invasive species' across the world.

Table S1 Number of endemic species in each of 34 biodiversity hotspots.

Table S2 Environmental variables.

Table S3 List of the 99 of 'the world's worst invasive species' with data sources and number of occurrences that were checked for each species.

Table S4 Standardized Euclidian distance thresholds (SEDt) calculated for each hotspot.

Table S5 Threatened endemic biodiversity due to climate change.

Table S6 Kolmogorov–Smirnov test results comparing the distributions of number of endemic species affected by climate changes for each value of z .

Table S7 Table of the rank for the 34 different hotspots according to number of endemic plant species for each hotspot (end.), the proportion of area protected by IUCN classification (I to IV) (PA), the percentage of climate loss (LCC), the potential number of invasive alien species in the future (IAS) and the percentage of future artificial land (LU) under A1B emission scenario.

Supplementary text S1 Methodological details about species distribution models.

BIOSKETCH

Céline Bellard works on the effects of global change (e.g. climate change, invasive alien species, and sea-level rise) on the future of biodiversity at a global scale. This paper formed part of her Ph.D. research at the University of Paris Sud.

Author contributions: F.C., W.T., C.L and C.B. conceived the ideas; C.L., B.L and C.B. performed the analyses; C.B. wrote the paper; all authors commented substantially the analyses and the manuscript.

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